



Simulating invasions in fragmented habitats: theoretical considerations, a simple example and some general implications

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Abstract

This contribution discusses two entirely different methodologies for spatially explicit modeling of population dynamics. A hybrid Petri net and a partial differential equation model are used to study the intrusion of a non-endemic species into patched habitats. A detailed comparison of both models based on an application for the Galápagos archipelago in terms of simulation results, methodology, as well as structure shows how different building blocks of ecological models can be. Results of the investigation give a detailed insight into the problem of scaling ecological models and the core question of what processes should be considered in which scale in terms of space, time or complexity and show that model structure depends on spatial configuration, and on the landscape pattern of the investigation area.

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1. Introduction

1.1. Mathematical heterogeneity in ecological models

Modeling ecological processes frequently lead to simulation models which may be characterized as mathematically heterogeneous. This means, simulation models consist of different mathematical structures such

as ordinary and partial differential equations, difference equations, integro-difference and integro-differential equations, stochastic elements, as well as matrix equations. One main reason for this is that ecological models are a product of interdisciplinary research. Models comprise approaches from biology, chemistry, physics, ecology, etc. Besides, physically based models—so called white box models are not available for every scale in terms of space, time or complexity. Ecological models comprise physical models as well as statistical and phenomenological models—black- and gray-box models. Finally, different modeling environ-

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ments or software-tools are used for model development (Seppelt, 2003).

An aim of each scientific theory is to come up with the most concise theory or a highly aggregated model that can reproduce the pattern and processes of a complex problem in a simple way. In this context, the aim of this contribution is to study the complex process of non-endemic species population dynamics by two different approaches. These examples are used to discuss questions on model complexity and the identification of building blocks.

1.2. Spatially explicit population dynamic models

Spatially explicit population models encompass the processes of:

1. Spatial spread of individuals by migration or distribution by wind or shears;
2. Population dynamics, and
3. Linkage with a spatially explicit habitat suitability model.

Different methodologies were presented in recent literature. Cellular automaton models seem to be the most common solution. Grid based approaches of handling spatial data seem to be the most favorite choice (Seppelt, 2003). This approach represents the landscape by a regular mesh of equally sized grids. Information exchange (migration, habitat suitability) is possible between two neighbored cells. A population model is attributed to each cell and parameterized by associated habitat parameters. This model of population dynamics may be of any kind (Matrix, Leslie Model), for example, see Richter et al. (2002), Söndgerath and Schröder (2002).

Other approaches vary in mathematical as well as spatial structure. Obviously, all models depend on the specific problem to solve. However, two distinct approaches can be identified when looking at the representation of the landscape: a continuous and a discrete parameterization of the habitat properties in space.

1.3. Aim and scope

The study is based findings that were very descriptive, presented in Seppelt (2002). In this contribution the focus is laid on the analytical

treatment of the system discussed and the implications for selecting appropriate model structures of spatially explicit population dynamics modeling.

For detailed analysis of the resulting mathematical structures depending on the selected method of regionalization, two entirely different modeling approaches are chosen to model spatially explicit population dynamics:

- Based on a modified McKendrick–Foerster equation, a partial differential equation (PDE) covering the physical processes of migration, growth and wind-spread solved by a dynamic finite element solver, and
- A phenomenological model using the meta-population approach by MacArthur and Wilson (1963), describing the processes of migration, growth, and spread solved by an event-based modeling environment using hybrid Petri nets.

The PDE model is a general mathematical formulation of a model with distributed parameters, which means that all parameters and coefficients are spatially referenced and depend on location. Cellular automaton models (CA) belong to this class of models. Structurally, CA models can be interpreted as a discretization of a PDE model with a fixed and constant spatial grain. However, the cellular automaton methodology allows several extensions that do not originate in a concise mathematical formulation. Because of this a thorough analytical treatment is difficult or even impossible. The explanatory value of PDE's is much greater.

Second, the Petri net model structure is the theoretical basis for any meta-population modeling approach (Wieting and Sonnenschein, 1995). Besides all other related rule-based models it allows the broadest spectrum of analytical treatment.

1.4. Species and study region

These models are applied to a non-endemic grasshopper species entering the Galápagos archipelago. For this simulation experiment the species *Oedipoda caerulea* is chosen. Different dynamic pattern of the models are studied and compared. The models are analyzed with respect to the analytical as well as numerical properties.

The investigations of in this contribution aim at a broad area of possible applications for species that show similar behavior in terms of population dynamics and migration. Nevertheless, we need quantitative information for the specification of model parameters for a selected species and the specification of a study area.

1.4.1. The Galápagos Archipelago

The Ecuadorian Galápagos islands were selected as a typical oceanic archipelago for the analysis of the models of insular zoogeography. The Galápagos archipelago is located 1050 km west of the shoulder of South America and contains 13 large islands, 6 small islands, and 42 islets with a total area of 8006 km². Isabela, the largest one, is 4278 km². The distances between the islands range from 4 to 68 km. The archipelago's vegetation ecosystem varies from rain forest to dry habitats with sparse vegetation. 378 species are endemic: 60% have been introduced by birds, 31% by wind, and 9% have been floated across the ocean. Nearly 800 species have been introduced by humans since 900 AD.

1.5. The blue-winged Grasshopper

Even if the Galápagos' ecosystems suffered from several alien species, intruding the archipelago, this is clearly an artificial simulation experiment. The blue-winged grasshopper, *O. caerulescens* (Linnaeus) is a palaearctic species with a distribution from North Africa and the Canary Islands in the south to Central Europe in the north. Eastwards the distribution reaches Southwest Asia and China (Harz, 1975). The xerothermophilous species can be found in regions from plains up to mountains with sparse vegetation. In 1996 it was observed that *O. caerulescens* have expanded their habitat from the island Rottumeroog to the island Borkum, both located in the North Sea. The distance between these two islands is 4.7 km (Appelt, 1996).

Thus, in this simulation experiment the Galápagos archipelago is suitable for *O. caerulescens*. It is in principle possible for *O. caerulescens* to reach the archipelago by passive transport and more important it is possible to settle and spread in this environment.

2. Modeling approaches

2.1. Hybrid Petri nets

A hybrid Petri net is used as underlying theoretical concept of dynamic meta-population models. With this methodology the spatial structure of the habitat network, population dynamics on suitable habitats, as well as stochastic migration can be described. Using the graphical modeling capability of Petri nets the framework offers an intuitive approach to the problems and support several steps of system analysis (Wieting and Sonnenschein, 1995).

A Petri net (PN) is a directed graph with two types of nodes, i.e. places p_i and transitions t_j . Alternate nodes are connected with arcs. Places are locations that hold information or data, within Petri net theory called "tokens". The transition nodes of the net transform the information carried by tokens. For each transition a rule is specified, that determines the conditions when all input tokens can be taken from the input places and tokens can be transformed to the output token. For standard Petri nets the number of input and output tokens is defined by weights, which are associated with the arcs. Petri nets are capable of simulating dynamic processes, especially event based simulations. Event based processes can be identified in ecological modeling. Examples are migration modeling in patchy or fragmented habitats or modeling population dynamics if distinct development stages of a population are considered.

The use of Petri nets in ecological modeling necessitates some extensions to the standard Petri net concept. These extensions concern

- Time marking of transitions, which allow different time periods for switching;
- Stochastic and dynamic behavior of transitions;
- Estimation of the number of output tokens by non-linear transition functions, as well as differential equations together with ordinary differential equation solver.

Seppelt and Temme (2001) presented this concept and introduced a detailed theoretical section on the formal definition of hybrid Petri nets.

2.2. Meta-population modeling of the Galápagos Archipelago

A meta-population model for a non-endemic species entering the Galápagos archipelago requires to set up models for the two processes of growth and migration. MacArthur and Wilson (1963) described migration from one habitat to another with the equation

$$n_{i,j} = \alpha e^{-\frac{1}{D}d_{i,j}} A(p_i) \frac{1}{\pi} \arctan\left(\frac{1}{2} \frac{\text{diam}_{i,j}}{d_{i,j}}\right) \quad (1)$$

where $n_{i,j}$ denotes the expected number of individuals probably moving from island p_i to island p_j in a chosen period of time (here 1 year). This number depends on the area $A(p_j)$ of the source habitat p_j , the “visible arc” of the destination island p_i derived from the arctan-function of the quotient of diameter of the destination island p_i taken at a right angle to the direction of p_i to p_j and the distance $d_{i,j}$ from island i to j . The exponential term introduces the decreasing success of migration with increasing distance $d_{i,j}$ from p_i to p_j , where D denotes a mean travel distance parameter and α the constant of proportionality, carrying the unit number of individuals per time and area. Fig. 1 visualizes the approach by MacArthur and Wilson (1963) and Eq. (1). The angle or visibility of the destination habitat β is estimated by

$$\beta = 2 \arctan\left(\frac{1}{2} \frac{\text{diam}_{i,j}}{d_{i,j}}\right)$$

If we divide this expression by the angle of a full-circle, 2π , we can derive the fraction of destination habitat that take part, with respect to all possible direction of migration, the full circle.

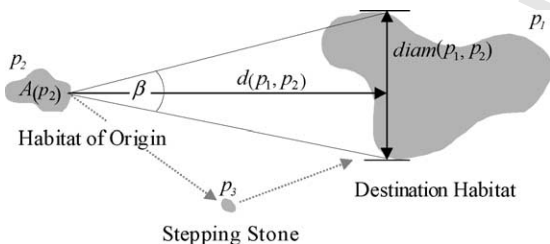


Fig. 1. Visualization of Eq. (1) and illustration of a probable location of a stepping stone habitat. Abbreviations: $\text{diam}_{1,2} = \text{diam}(p_1, p_2)$ and $d_{1,2} = d(p_1, p_2)$.

For the growth of the grasshopper population on an island p_i the well-known logistic growth function is assumed:

$$\frac{dP(p_i)}{dt} = f(p_i) = rP(p_i) \left(1 - \frac{P(p_i)}{C(p_i)}\right) \quad (2)$$

$P(p_i)$ denotes the population on island p_i . Habitat suitability may be introduced by habitat dependent growth rate r and/or habitat dependent carrying capacity $C(p_i)$. The growth rate r is assumed to be constant for the entire study area. The carrying capacity depends on the size of the island $C_i \propto A(p_i)$.

Fig. 2 shows a map of the larger islands of the Galápagos archipelago overlaid by the Petri net developed to estimate the expansion and population dynamics. The places represent the species' population on an island. The transitions with rounded corners are connected to a logistic growth model (non-standard Petri net extension).

The arcs between the islands in the Petri net specify the probability of migration from one island to another according to Eq. (1). The parameters of Eq. (1) such as diameter, distance or area are obtained from the digital map of the Galápagos archipelago using a Geographic Information System (GIS). Another non-standard extension of the Petri net is the use of stochastic transitions for the migration process with a uniform distribution and the expectancy value $1/n_{i,j}$.

2.3. Dynamic behavior of Petri net model

The PN-model is an event-based model. Each transition can perform its operation (move token from all input places to all connected output places, see Fig. 2) if all conditions are fulfilled. For the meta-population model these are two conditions

- A sufficient number of individual has to be available for migration from the source island;
- Available space must be present in the destination island ($P(p_i)$ smaller than carrying capacity).

A dynamic simulation performs the following steps:

- A random number is generated (in each time-step). Based on this random number migration from island p_i to p_j happens with the probability $1/n_{i,j}$.

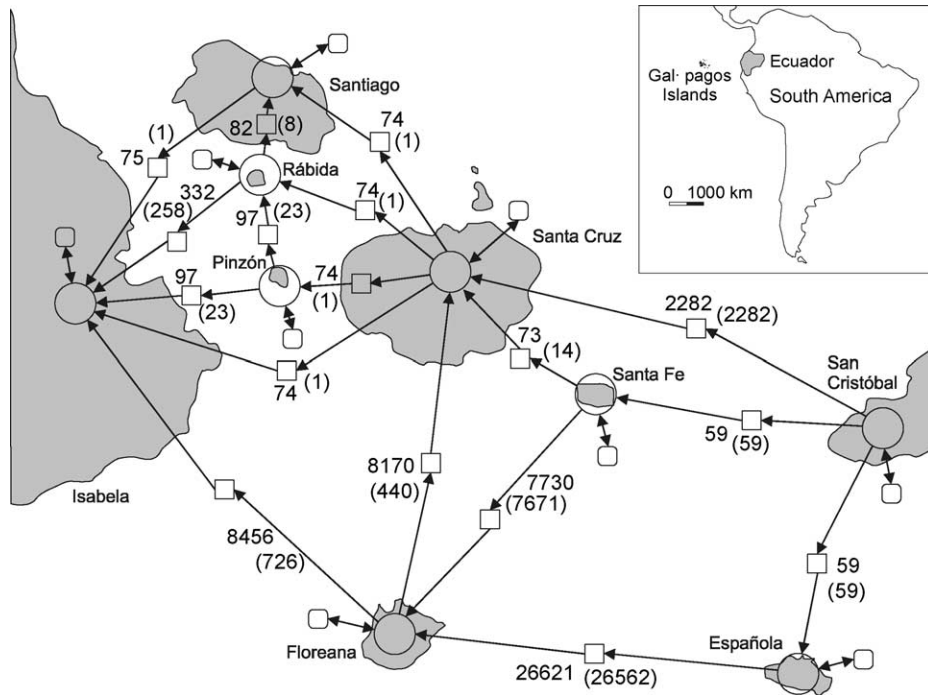


Fig. 2. Map of Galápagos archipelago with the Petri net. The numbers at the arcs denote the first possible colonization of an island. The numbers in brackets denote the average time in years grasshoppers need to migrate.

- In each time-step the hybrid transitions for growth perform their operations (solve Eq. (2)), if tokens are available at the input place, e.g. a positive abundance at the considered island (boxes with rounded edges in Fig. 2).

The resulting simulation is a realization of a stochastic event-based process. Several simulations are to be performed to derive a general pattern of the simulation (Monte-Carlo simulation).

2.4. Partial differential equation

Considering the processes of migration, dispersal and growth continuously with distributed parameters and variables leads us to the formulation of partial differential equations. As mentioned above any discretization of this concept can be interpreted as a cellular automaton with a fixed geometric structure.

Following for instance Henson (1999) the process of spatially explicit population dynamics of a

population P can be described by the partial differential equation

$$\frac{\partial P}{\partial t} - \nabla \cdot (D \nabla P) + v \cdot \nabla P = f(P) \quad (3)$$

with the notations

P	population at location $\vec{x} = (x, y)$ depending on time t (individuals per area)
D	coefficient of migration
v	vector of wind
f	function for non-spatial process of growth, mortality, etc.
∇	estimates the spatial derivative of the state variable $P(x, y, t)$, e.g. calculates the $(\partial/\partial x, \partial/\partial y)$ from the function it is applied on (Nabla operator).

Information on the geometry, topology and the habitat properties of the study area is introduced to the model as follows: For the ocean the function f

describes a process of mortality. On an island p_i the function f defines a process of logistic growth with the rate r with a habitat dependent carrying capacity, Eq. (2)

$$f(P) = \begin{cases} -\mu P & \text{open water} \\ rP \left(1 - \frac{P}{C_i}\right) & \text{for island } p_i \end{cases} \quad (4)$$

The coefficient of migration is assumed to be constant over the entire study area and is equal to the average area a grasshopper can cover with its movements within a considered time step. Extensions can easily be introduced to the model. The diffusion term D may depend on gradients in the landscape to cover the process of migration to more suitable habitats. To be comparable to the approach used for the PN-model these topics are neglected.

Boundary conditions have to be defined for the arbitrarily defined boundary of the study area on the open ocean. A boundary condition of Neumann-type is assumed

$$\frac{\partial P}{\partial \vec{n}} = 0$$

This denotes no change of population at the boundary of the investigated area, e.g. the population P near the boundary of the study area is equal to its associated location outside the study area.

A tool for numerical solving partial differential equations is required to derive solutions of Eq. (3). FemLab[®], an extension to MatLab[®] (Comsol, 2001), is used. The tool bases on the technique of finite element methods (FEM). An important step of pre-processing is to set up of the geometry of the study area. Based on a digital map of the Galápagos archipelago a finite element mesh was generated using a GIS, cf. Fig. 3. These parameters of Eq. (3) were specified using the information on habitat size derived from the GIS.

2.5. Parameterization

The parameters D , C_i and r are required in the two modeling approaches equally, Eqs. (2)–(4). The growth rate is derived based on considerations from Yang and Sykes (1998) for insects, who assume a growth rate of 0.5 – 1.1 day^{-1} which yields $r = 0.06 \text{ a}^{-1}$. The modeling approaches use the logistic growth equation with identical parameters.

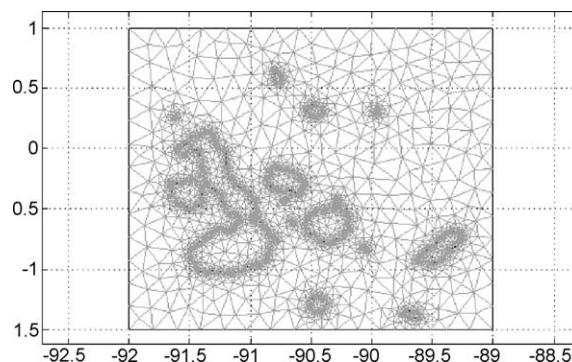


Fig. 3. Finite element mesh for Galápagos archipelago. On x - and y -axis latitude and longitude are noted in degrees. The adaptively generated FEM mesh consists of 15,437 triangles.

However, this sub-model is incorporated in a totally different model-context. Model analysis needs to focus on the resulting pattern—their differences as well as similarities—in the two modeling approaches in time as well as in space.

The minimum area of a suitable habitat for *O. caerulescens* is 500 – 600 m^2 . An average population density of 1 adult per 10 m^2 has been observed (Appelt, 1996). Based on these observation the carrying capacity C_i of an island p_i is calculated by $C(p_i) = \gamma(p_i)$ with $\gamma = 0.1$ (number of individuals per reference area) and the area $A(p_i)$ of island p_i . Additional abiotic or biotic influences to the carrying capacity may be added using habitat suitability models to this approach.

These grasshoppers move about 10 m daily on average, but migration distances of 800 m per day have been recorded (Appelt and Poethke, 1997). From these observations on the blue-winged grasshopper the $D = 6 \text{ km}^2 \text{ a}^{-1}$ was selected from a range of 2 – $17 \text{ km}^2 \text{ a}^{-1}$. The underlying assumption for the derivation of the dispersal coefficient D from the mean traveling distance is that the Euclidean metric is chosen as distance measure in a two-dimensional space (the area of migration). Using digital maps of the Galápagos archipelago in a GIS for the estimation of $A(p)$, $d(p_{ij})$, and $\text{diam}(p_{ij})$.

Wind might also determine the maximum dispersal distance. By incorporating advection setting a slight easterly south-easterly wind of 1 m s^{-1} the vector of convection v is defined and a constant ‘drift’ of the species into a certain direction is assumed. However,

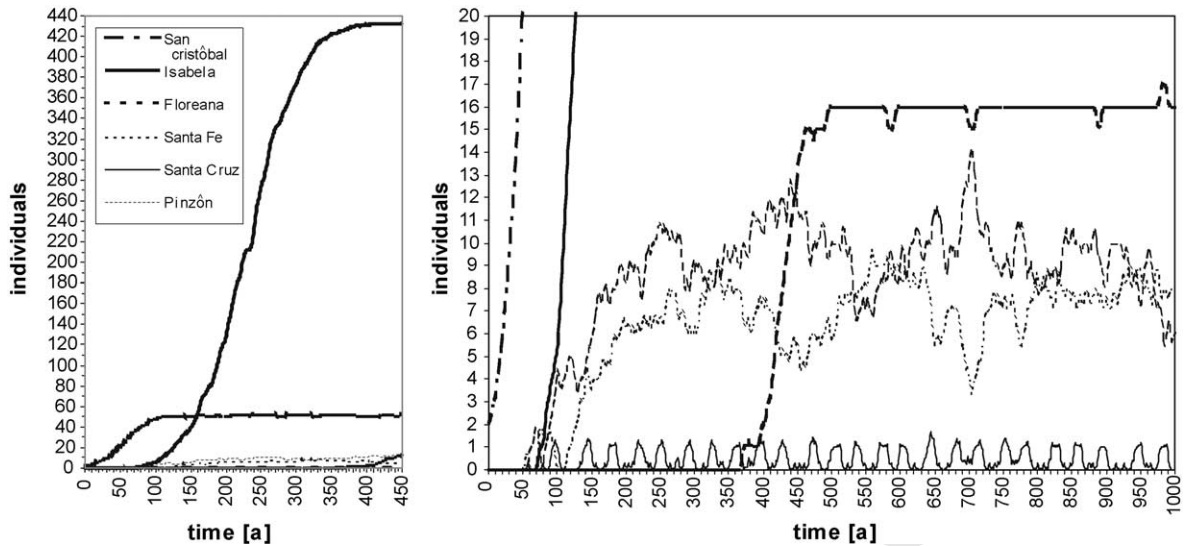


Fig. 4. Population dynamics on different islands. The left figure shows the population size on the larger, the right figure shows the populations of smaller possible stepping stone islands.

in the case, a grasshopper is in patch, it would not migrate and thus it is not affected by wind. However, we use this as a case study. Several other approaches can be found in recent literature that use diffusion–advection equation with modified dispersal parameters introducing habitat suitability as well as population dispersal, etc., for instance, see Henson (1999). The Petri net implicitly makes use of this information by enabling migration paths in the directions from south to west to north only. Mortality coefficient set to $\mu = 0.0003 \text{ a}^{-1}$.

Thus, parameterization of the models is equivalently for the parameters growth rate, carrying capacity and dispersal. The models differ in the methodology of how spatial processes are incorporated into the model.

3. Results

3.1. Dynamic simulation

First topic of interest is the dynamic behavior of the models. A starting population at the island San Cristóbal gives the initial condition for both model types. Running the hybrid Petri net results in a set of time series with the abundance values for each

island. Fig. 4 displays the results of a typical simulation run. Left part of the figure shows the populations on the larger, the right part shows the population sizes (below 20) of the smaller islands. Temporarily extinction on these islands is possible. Nevertheless these islands are important to support survival of the meta-population of the entire archipelago. These islands are called *stepping stones* and enable or help individuals to migrate from one larger island to another. Finally, the main island Isabela carries a population half of the carrying capacity after 250 years.

The results of the partial differential equation model are entirely different with respect to the data structure. This model calculates abundance values for an arbitrary location within the study area (89° to 92° W, 1.5° S to 1° N): it is a full spatially explicit model. Contour plots are used to display the population, c.f. Fig. 5.

With the underlying assumption on migration and dispersal we get small but positive population sizes for ocean areas. However, this is essential to allow migration to a different island. Extinction on smaller islands is possible. On these islands the process of migration overwhelms the growth process. Focusing on the population dynamics on the islands, the simulation results of both model types are comparable.

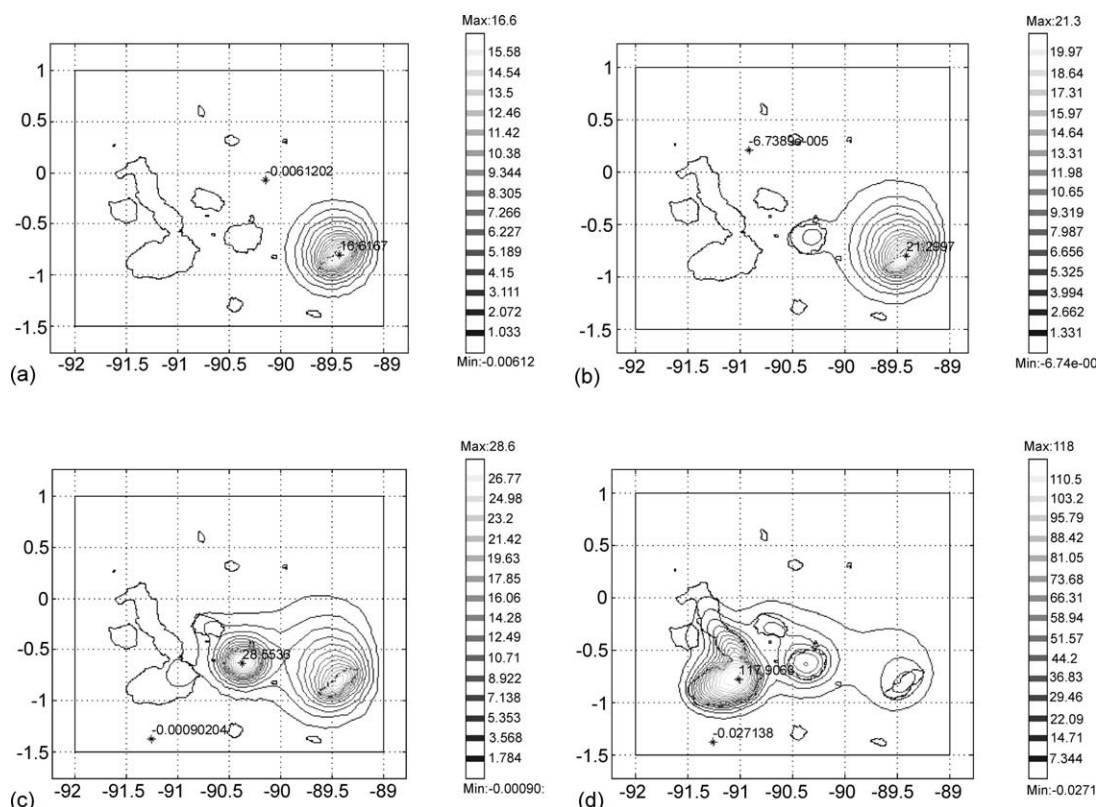


Fig. 5. Simulation results of spatially explicit population dynamics of grasshopper species in Galápagos archipelago based on partial differential Eq. (3). Four different time step of the simulation are shown: (a) $t = 50$, (b) $t = 100$, (c) $t = 150$, (d) $t = 200$ years.

For instance, on Isabela Island a population half of the carrying capacity is reached after 250 years. Population sizes and migration times are comparable. However, this comparison can only be interpreted qualitatively. The partial differential equation model gives a continuous distribution of grasshoppers for one time step. Due to the continuous definition of the state variable P the time the first grasshopper reaches an island can be identified by a definition of a threshold value (a certain population) only. A comparison to the discrete values resulting from the Petri net simulation is difficult, which—on the other hand is a stochastic model, c.f. Fig. 4.

3.2. Numerical analysis

A second important topic to look at is the qualitative results on meta-population stability and migration pathways. Which islands are respon-

sible for a spatial spread of the population over the entire islands? Which are the migration pathways? Both models give answers to this question.

Using the Petri net the vector of the switching frequencies of every transition is one starting point for the analysis. Based on this *net comitant*, a pathway analysis can be derived. Fig. 6 shows a GIS-based graphical representation of this Parikh-vector analysis. The most frequent stepping stone islands can be identified (Santa Fe, Pinzon). However, direct migration pathways are also used, e.g. San Cristobal to Santa Cruz.

Using the partial differential equation model, these results are derived by a “grasshopper”-tracking analysis, a function most FEM-solver programs are capable of, usually known as particle tracking. A general statement like the one we get from Fig. 6 cannot be derived from the PDE model.

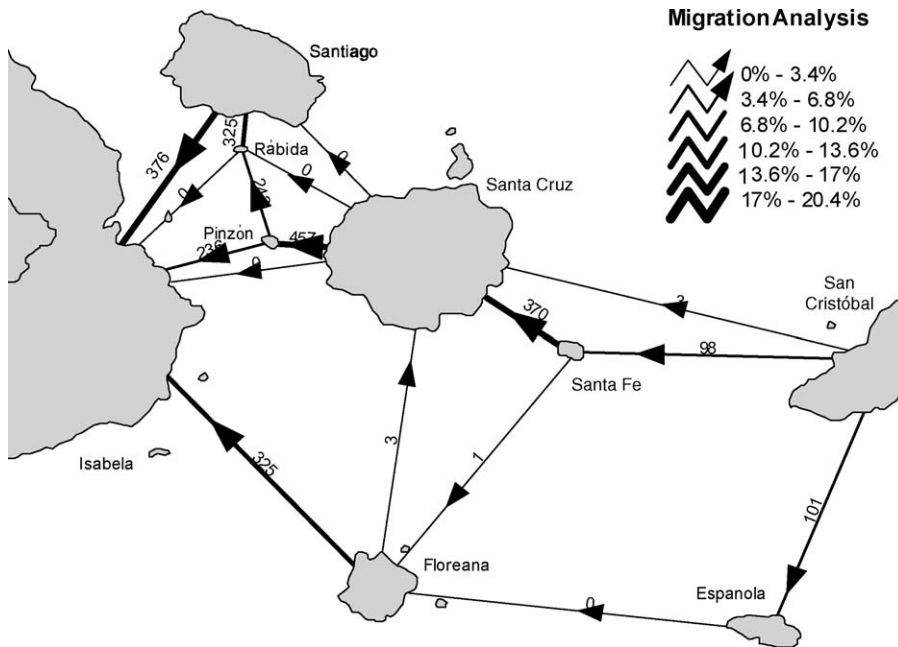


Fig. 6. Analysis of migration pathways derived from Petri net analysis.

3.3. System analysis

The striking result up to this point is that the results of both modeling methodologies are similar and comparable even though the models originate from entirely different approaches: the more phenomenological PN-model and the physically motivated PDE model. The upcoming question is, is it possible to identify common structures, so called “building blocks” of the models?

Analyzing intrinsic properties of the models can approach the questions raised. One has to distinguish two different domains of the modeling approaches. First, population dynamics on an island are equal for the two models, if we neglect migration processes on a sub-island scale. Simulation results would differ if habitat maps of each island may define habitat suitability and diffusivity. For the given problem both models use a logistic growth curve for the population dynamics on each island.

The major difference of the two models is the modeling of migration from one habitat to another. The core task is to identify a relationship between the empirical equation from MacArthur–Wilson (Eq. (1)) and the partial differential equation for open water. To

cope with this task, some simplifications are made. We consider a spatially one-dimensional problem, e.g. a transect from one island to another, and we assume that the source-habitat is close to the habitat capacity P_0 and P_0 individuals are ready to leave an island.

Under these considerations the analytical solution of Eq. (3) with the right hand side according to the open water case of Eq. (4) is given by (see Appendix A)

$$P(x, t) = P_0 e^{-\mu t} \operatorname{erfc} \left[\frac{x}{2\sqrt{Dt}} \right] \quad (5)$$

From this we can calculate a 50% population iso-surface as a function of location x and time t , e.g. a function that specifies how far 50% of the population P_0 migrated depending on the time by solving

$$\exp[-\mu t_{1/2}] \operatorname{erfc} \left[\frac{x(t_{1/2})}{2\sqrt{Dt_{1/2}}} \right] = \frac{1}{2} \quad (6)$$

in t and x .

We can calculate the time needed for a 50% probability of a location x to be reached by the population P based on Eq. (1). Without loss of generality we assume a circled island with the radius 1 and replace the distance of two island by x ($d_{1,2} = x$).

According to Eq. (1) the expected number of migrants within time t is $n_{i,j,t}$. To obtain the 50% isosurface the expected population should be half of the source population which is given by $A(p_i)$. Thus it yields $n_{i,j,t_{1/2}}$ needs to be equal to half of $A(p_i)$. Without loss of generality we can assume $A(p_i) = 1$ obtaining

$$t_{1/2} = \frac{1}{2} A(p_i) n_{1,2}^{-1} \\ = \frac{1}{2} \left(\alpha e^{-\frac{1}{D} x(t_{1/2})} \arctan \left(\frac{1}{x(t_{1/2})} \right) \right)^{-1}$$

Analogously we can derive the iso-surfaces of the 10% and 90% level.

Fig. 7 displays the results of this analysis. The maximum distance 10, 50 and 90% of a population could migrate is plotted against time. First, the 10 and 50% curves of both models are comparable and similar especially for simulation runs up to time steps of $t < 5$ years. Major differences are identified for the 10%-curve for $t > 5$ years. However, this similarity is striking, as this analysis compares a phenomenological and a physical model.

Difference in the structural behavior of the model is identified for the 90% curve. The PDE-model estimates a much lower migration distance for 90% of a population compared to the PN-model. Second, from the PDE model a maximum migration distance or 1 km for 90% of the population can be derived. This pattern becomes much clearer, if the maximum migration distances for a time range up to 75 years are considered, see Fig. 7 lower part. All iso-lines resulting from the PDE model show a maximum migration range. This is due to the fact, that the PDE model assumes a positive mortality rate for the open water regions. The parameter specification of mortality and dispersal determines the maximum migration distance in the PDE-model. As mortality is neglected in the PN-model, the steady-state of this model will be a sustainable population on the entire archipelago independent from the dispersal coefficient and the network connectivity, for t to infinity.

PDE models are not appropriate to model long distance transport. This could be an obvious conclusion of these findings. However, this conclusion neglects, that smaller abundances (below 10% of the migrating population P_0) can reach habitats further

away. However, an appropriate conclusion would be to state that PDE models are inappropriate to model dispersal in highly fragmented landscapes with long distances between the habitats. Additionally strong gradients such as suitable (island), unsuitable (open water) may yield in numerical problems, whereas PDE models can perfectly be applied to landscapes with continuously changing habitat suitability.

Analogously, there is also a limitation in applicability of the PN model based on the MacArthur and Wilson (1963) approach (Eq. (1)). If suitable habitats are spatially located such that $\text{diam}_{i,j}/d_{i,j}$ result in large numbers (either because the destination habitat is large, or because the distance is small), probability migration success remains constant (due to the non-linearity in Eq. (1)). In spatially dense distributed habitats Eq. (1) may be inappropriate to simulate the migration process adequately.

4. Discussion

Quantitative similarity of modeling approaches depends on the chosen parameters. To achieve generality of these results, derivation and estimation of parameters was reported in a reproducible way. On the other hand, the results of the system analysis (see previous section) were obtained from analytical treatments. Thus, the results hold true for all similar modeling approaches and methodologies.

Both modeling approaches solve the problem in hand. Both methodologies show their merits and their disadvantages. For a detailed comparison of the two modeling approaches, Table 1 gives a summary of different aspects.

In terms of scientific theory, the partial differential equation system is the more concise one. It uses a more aggregate model with a broad range of resulting explanations. This model collects the processes into one core equation. On the other hand, with this model we can run into more problems concerning numeric methods and interpretation. For instance, how shall we interpret positive population values for open water regions? Additionally a statistical analysis in terms of migration pathways is not possible. These results were obtained from the meta-population model (PN) only.

In recent publications one can observe that ecological modeling studies more and more moves

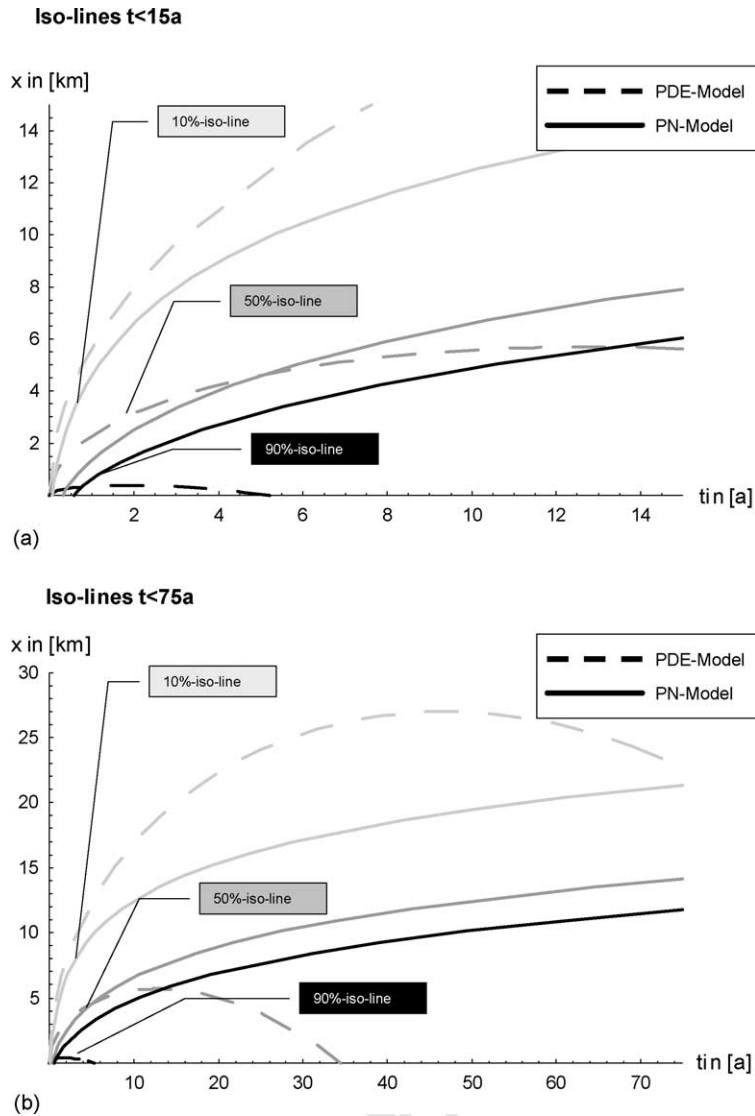


Fig. 7. Results of analytical treatment of open water model: 10%-, 50%-, and 90%-iso-surfaces of open water migration. Parameters are $D = 6$, $\mu = 0.03$.

towards a numerical treatment of complex model systems applied to real landscapes (Seppelt, 2003). In this publication it was shown that, both numerical modeling as well as analytic treatment is essential for an understanding and the analysis of the processes. Within this scope mathematical heterogeneity is an inherent property of ecological models. Modeling biological systems requires the development of

mathematically heterogeneous systems. This is either because of temporal or spatial processes show both, a discrete and a continuous behavior. Note that our perception of a process recognized as discrete or continuous depends also on the considered (spatial or temporal) scale. Hybrid models based on different mathematical modeling languages are the common result in ecological modeling.

Table 1

Comparison of both modeling methodologies

	Petri net (PN)	Partial differential equation (PDE)
Processes		
Dynamic	Continuous (growth)	Continuous
Spatial	Stochastic, discrete, event-based (migration)	Continuous
Data		
Topology of habitats	Topological relation between the habitats/islands is the only information implemented into the Petri net	No information on topology of habitat patches deducible from FEM mesh
Geometry of habitats	Only aggregated indication on the geometry of the archipelago are fed into the PN-model: distance, diameter of a habitat	FEM mesh directly derived from habitat borders, imported from GIS
Landscape (spatial configuration of habitats)	Appropriate for modeling highly fragmented and patchy habitats No change in migration probability, if habitat plots are spatially close	Simulation of highly fragmented landscapes for long-range migration difficult Appropriate to simulate continuous varying habitat suitability
Analysis results (analytical, numerical)	Stochastic analysis, Monte-Carlo simulation Event based model Stepping Stones Frequency of colonization	Numerical solution by FEM using adaptive mesh generation Experimental migration pathways Maximum migration distance Minimum connectivity distance Non-zero abundances for open water regions
Classification	Empirical approach	Foundation on migration- and growth-models

5. Outlook

Many authors suggest that integration of different (preferably existing) models is the appropriate way to build complex models for a process of interest. An integration requires at least a flexible (possible object-oriented, as suggested by Villa (2001)) documentation together with a framework of data exchange to assist model coupling, c.f. Maxwell and Costanza (1997). Besides these more technical aspects knowledge on the suitability of model integration is required. The presented case study gives some hints on the spectrum of problems one is faced with when aiming at integration or coupling of different models.

A general conclusion from this study is that a theoretical foundation of ecological modeling as requested by different authors (Jørgensen, 1999; Wu and Hobbs, 2002), which can cope with the inherent properties of complexity and heterogeneity necessitates to treat model systems as modular toolboxes with a large spectrum of different “building blocks” and the ability of an analytical treatment of each module as

well as a precise specification of the domain of the model. This domain not only has to be defined by the spatial and temporal scale of the model. It has to cope also—as we have seen in this study with the spatial configuration of the investigation site. This should be considered by recent developments and case studies on model integration presented for instance by Maxwell and Costanza (1997), Villa (2001), and Muetzelfeld and Massheder (2003). The spectrum of the available types of building blocks in these examples is still very limited, for instance, the restriction to ordinary differential equations. Such a toolbox would need to cope with PDE's as well as well known ODEs, Petri nets, or delay differential equations.

Appendix A

The analytical solution of Eq. (3) for the open water areas (cf. Eq. (4)) can be derived from the analytical solution of the convection–dispersion equation. We assume a constant diffusion coefficient $D(x) = D$ and

consider (without loss of generality) the spatially one-dimensional case.

$$P(x, t) = \frac{\bar{P}}{2\sqrt{\pi Dt}} \exp \left[-\frac{(x - vt)^2}{4Dt} - \mu t \right]$$

solves Eq. (1) with the right-hand side $f(P) = -\mu P$. x denotes the (positive or negative) distance from an initial population \bar{P} assumed as a point-source in the origin $x = 0$. The solution for a population P_0 at origin $x = 0$ constantly migrating over the open water area is calculated by setting $\bar{P} = P_0 d\xi$ and solving

$$P(t, x) = \frac{P_0}{\sqrt{\pi Dt}} \int_x^\infty \exp \left[-\frac{(\xi - vt)^2}{4Dt} - \mu t \right] d\xi.$$

Substituting $\eta = \xi/(2\sqrt{Dt})$ solves the integral using the error-function complement and the result using in Section 3.1 is obtained:

$$P(x, t) = P_0 e^{-\mu t} \operatorname{erfc} \left[\frac{x}{2\sqrt{Dt}} \right]$$

References

- Appelt, M., 1996. Elements of population vulnerability of the bluewinged grasshopper *Oedipoda caerulea*. In: Settele, J., Margules, C.R., Poschlod, P., Henle, K. (Eds.), Species Survival in Fragmented Landscapes. The GeoJournal Library, vol. 35. Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 320–323.
- Appelt, M., Poethke, H.J., 1997. Meta-population dynamics in a regional population of the bluewinged grasshopper (*Oedipoda caerulea*; Linnaeus, 1758). J. Insect Conserv. 1, 205–214.
- Comsol, A.B., 2001. FEMLAB, Users and Reference Manual. Tegnérsgatan, Stockholm, Sweden.
- Harz, K., 1975. Die Orthopteren Europas, vol. 2. W. Junk, The Hague.

- Henson, S.M., 1999. A continuous, age-structured insect population model. J. Math. Biol. 39, 217–243.
- Jørgensen, S.E., 1999. State-of-the-art of ecological modeling with emphasis on development of structural dynamic models. Ecol. Model. 120, 75–96.
- MacArthur, R.H., Wilson, W.O., 1963. An equilibrium theory of insular zoogeography. Evolution 17 (4), 373–387.
- Maxwell, T., Costanza, R., 1997. A language for modular spatio-temporal simulation. Ecol. Model. 103, 105–113.
- Muetzelfeld, R., Massheder, J., 2003. The Simile visual modeling environment. Eur. J. Agron. 18, 345–358.
- Richter, O., Zwerger, P., Böttcher, U., 2002. Modelling spatio-temporal dynamics of herbicide resistance. Weed Res. 42, 52–64.
- Söndgerath, D., Schröder, B., 2002. Population dynamics and habitat connectivity affecting the spatial spread of populations—a simulation study. Landscape Ecol. 17, 57–70.
- Seppelt, R., 2002. Avenues of spatially explicit population dynamics modelling—a par excellence example for mathematical heterogeneity in ecological models? In: Rizzoli, A.E., Jakeman, A.J. (Eds.), Integrated Assessment and Decision Support, Proceedings of the First Biennial Meeting of the International Environmental Modelling and Software Society 1. pp. 269–274.
- Seppelt, R., 2003. Computer-based Environmental Management. Wiley/VCH, Weinheim, New York, 304 pp.
- Seppelt, R., Temme, M.-M., 2001. Hybrid low level Petri nets in environmental modeling—development platform and case studies. In: Matthies, M., Malchow, H., Kriz, J. (Eds.), Integrative Systems Approaches to Natural and Social Sciences. Springer, Berlin, pp. 181–202.
- Villa, F., 2001. Integrating modelling architecture: a declarative framework for multi-paradigm, multi-scale. Ecol. Model. 137, 23–42.
- Wieting, R., Sonnenschein, M., 1995. Extending high-level Petri nets for modeling hybrid systems. Syst. Anal., Model. Simulat. 18/19, 259–262.
- Yang, M.D., Sykes, R.M., 1998. Trophic-dynamic modeling in a shallow eutrophic river ecosystem. Ecol. Model. 105, 129–139.
- Wu, J., Hobbs, R., 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecol. 17, 355–365.